In Memoriam

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IN MEMORIAM: CHARLES GALD SIBLEY, 1917–1998

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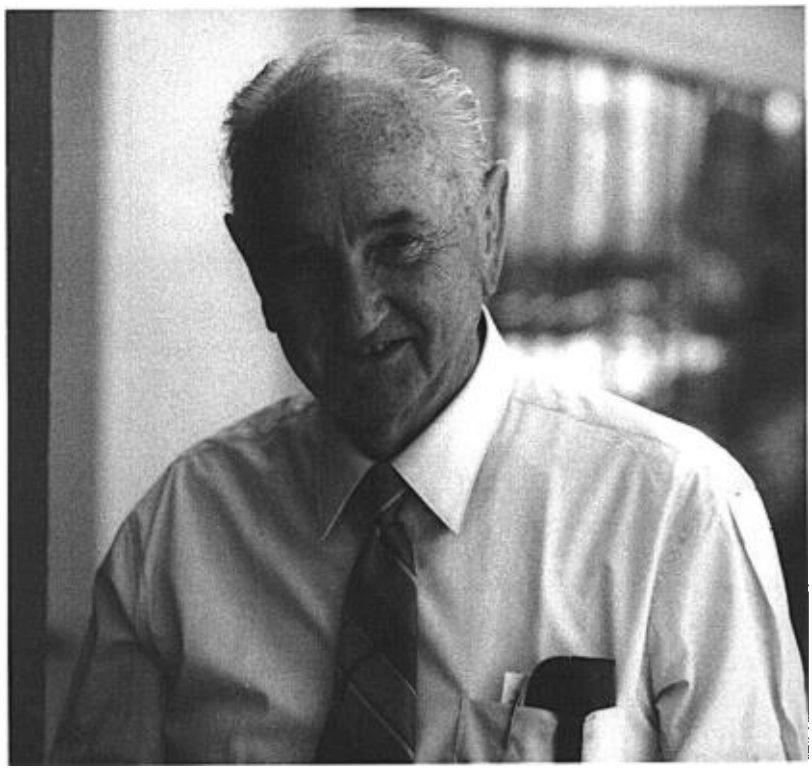

CHARLES GALD SIBLEY, 1917–1998

(Photograph taken in August 1987. Photo by Peter Stettenheim.)

Charles Gald Sibley was born in Fresno, California, on 7 August 1917; he died at age 80 in Santa Rosa, California. He was no small town boy who simply moved upstate, however. Between his early years in Fresno and his ultimate move to Santa Rosa, Charles traveled the world to conduct and report on his research, and he rose to prominence in the scientific community. He became one of the leading ornithologists during the last half of the 20th century, was one of the founders and a major player in the emerging field of molecular systematics, and contributed significantly to our knowledge of the evolutionary relationships

among the higher avian taxa. Charles Sibley is survived by Frances, his wife of 56 years, whom he met as Frances Louise Kelly, and their daughters Barbara Susanne, Dorothy Ellen, and Carol Nadine.

Charles joined the AOU in 1939, became an Elective Member in 1949, and a Fellow in 1955. He served as Treasurer for 11 years from 1953 to 1963, and as President during the 1986–1988 term. Before becoming President, Charles served twice as Vice President and was elected to several terms on the Council. In 1971, he was given the William Brewster Memorial Award by the AOU, and in 1986 both he and Frances became Patrons of the organization he had served so often and so well.

In addition to his AOU activities, Charles was a Secretary of the Cooper Ornithological Society, a Fellow or Corresponding Fellow of six foreign societies, and an officer or council member of five societies. From 1958 to 1962 he served as the Secretary General of the 13th International Ornithological Congress, and from 1986 to 1990 he was President of the 20th International Ornithological Congress. Altogether he was a member of about 15 scientific societies, including all major ornithological societies of the USA as well as Deutsche Ornithologen-Gesellschaft, Société Ornithologique de France, Asociación Ornitologíca del Plata, and Suomen Lintutieteellinen Yhdistys. He served on the editorial boards of *Evolution, Journal of Molecular Evolution,* and *Molecular Biology and Evolution.*

Charles was associated with six universities over the course of his academic career. His first appointment was a one-year Assistant Professorship in 1948 at the University of Kansas. A year later he returned to his native state to join the faculty of San Jose State College (now California State University at San Jose) as an Assistant Professor of Zoology. In 1953 he went to Cornell University as Curator of Birds and Associate Professor of Zoology in the Department of Conservation. During his 12 years there, Charles advanced to Professor, taught ornithology to overflowing classes of both graduate and undergraduate students, developed Cornell's scientific collection of bird specimens, and mentored nine graduate students and one postdoctoral fellow. In 1959–1960, he took a sabbatical year at Oxford University as a Guggenheim Fellow. Back on the Cornell campus during the summer of 1962, he oversaw the activities of the 13th International Ornithological Congress. Broadly speaking, his research during the Cornell years dealt with hybridization between species pairs and the molecular systematics of avian orders and families.

In 1965, Charles moved to Yale University as a Professor of Biology, the William Robertson Coe Professor of Ornithology, and Curator of Birds of the Peabody Museum of Natural History. In 1970, he was appointed Director of the Peabody Museum of Natural History. During his years at Yale, Charles advised another seven graduate students and three postdoctoral fellows. In 1986, he was elected to the National Academy of Sciences. That same year, Charles retired and was named a Professor Emeritus of Yale University. Later that year, he and Fran again moved back to California. There he became affiliated with San Francisco State University as a Dean's Professor of Science and Professor of Biology. In 1988, Charles and his colleague, Jon E. Ahlquist, received the Daniel Giraud Elliot Medal from the National Academy of Sciences in recognition of their contributions to our knowledge of avian systematics, and in 1991 Charles was awarded the Alessandro Ghigi Medal by the National Institute of Wildlife Biology, of Italy. His final appointment occurred in March of 1993, after moving to Santa Rosa. There he was named Adjunct Professor of Biology at Sonoma State University, in part so that he could have continued access to his extensive personal library that he had given to the university.

Charles' intellectual intensity and excitement touched the lives of many of his contemporaries, in ways both good and bad, and he influenced several generations of students. Few ornithologists, however, have so polarized their students and colleagues. Ultimately, his greatest influence may be the transmission of his ideas and intellectual fervor to students, which he did with an evangelical intensity, sometimes threatening his wrath, but usually with the grace of a master communicator.

Charles was exceptionally well organized and was blessed with a fine intellect and an unyielding belief in himself. However, those at the receiving end of one of his famous verbal debates or attacks may not have looked beyond their own bruised egos to appreciate his finer qualities. He was a generous person, giving

freely and frequently of his time to students and colleagues, particularly if it involved discussions of science. He took pride in his broad understanding of biology and its processes, but he stuck to his own beliefs and understanding of biological "facts" until presented with unequivocal information that he was wrong. Then, immediately, he would champion the new information, never looking back to dwell on the fact that he may have been wrong about some fact or in his understanding about how a process worked. This contrary nature of being dogmatic on the one hand, while always welcoming new information on the other, made it difficult for some people to deal with Charles and his science, but for his students he was an endlessly variable, fascinating, and challenging role model.

In his conversations with students and colleagues, Charles could generate great excitement about the potential of his research. He delighted in invitations as plenary or keynote speaker, and he occasionally organized "minisymposia" at scientific meetings where he and his students would give papers updating their current research. Throughout his career he attracted individuals upon whose lives he made an indelible mark. The two of us are cases in point. We can also cite many of the individuals who studied under him, both at Cornell and Yale, either as graduate students or as postdoctoral fellows. Among them are four AOU Elective Members, eight AOU Fellows, an AOU Secretary, an Editor of *The Auk,* and an AOU Treasurer.

Every project that Charles undertook demonstrated his talent for enlisting the help of an extraordinary diversity of people and expertise. For example, in 1961 when he first set his sights on setting up a DNA-DNA hybridization facility at Cornell, he sent one of us (KWC) to Bethesda, Maryland, to learn the techniques from the three biochemists who had just months earlier developed the methodology. In 1966, when Charles wanted avian blood samples from European species, he contacted a number of friends who would be at that year's International Ornithological Congress in Oxford, asking for their aid in that early work on hemoglobin. And Charles was never hesitant to enlist knowledgeable individuals well outside academia in order to achieve his goals in field work.

No field work of his illustrates this better than the immense effort he put into planning for the 1969 NSF expedition to Papua New Guinea aboard the research vessel *Alpha Helix.* A year prior to that expedition, Charles and Professor George A. Bartholomew (from UCLA) made a comprehensive assessment of the potential field facilities, logistics, and personal contacts in that vast region. There they enlisted the cooperation and help of an amazing group of individuals, some of whom were local officials, administrators, ministers of either the Lutheran or Catholic churches, an archbishop, ranchers, pilots, local scientists and educators associated with the Australian National University facilities, members of the Australian Bush Patrol, telegraph operators, directors of sanctuaries, and native Papua New Guineans.

One extraordinary bit of organization occurred while collecting *Aplonis* starlings on the Bismark Archipelago in 1969. The collecting party included Charles and two of his postdoctoral fellows, Andrew Ferguson of Ireland and KWC. The setting was the school yard of a Catholic Mission outside of Rabaul. The object of the mission was the collection of 20 inhabitants of a large colonial nest hanging near the entrance to the school, while minimizing the effect on the school's activities. After a brief discussion with the school's principal, Charles enlisted him in our plan, and instantly the collecting corps had grown several fold. While the majority, but naive, portion of the group waited excitedly inside the school, Charles, Andy, and Kendall positioned themselves on different sides of the nest tree. There they waited a few moments until various branches on the nest tree had 5 to 10 birds lined up waiting to enter the nest. Then on the count of three . . . BLAM! The students rushed outside to help gather up the wounded, and in less than 10 minutes the successful collecting party was on its way back to an ANU house in Rabaul, where the sample preparation was completed and specimen preparation was soon underway.

Charles published extensively throughout his life, from his late teens until his final days, with his research spanning the fields of paleontology, evolutionary biology, and molecular systematics, with some population genetics thrown in for good measure. Broadly speaking, his research was associated with his three major interests: fossil birds, hybridization be-

tween species pairs, and the systematics of higher avian taxa based on molecular data. The results of his studies were published in 113 refereed articles, 8 book chapters, and 7 book-length monographs.

As a youngster, Charles was an avid birder who kept precise records of his observations very early on. He was introduced to natural history by reading John Burroughs and Ernest Thompson Seton. A close friend, Robert Failing, encouraged his interest in birds, and a high school teacher, Jean M. Nelson, was particularly supportive of his interests in natural history, helping Charles to found the natural sciences club at Oakland High School. In the mid 1930s, as an undergraduate at the University of California, Berkeley, he gravitated to the Museum of Vertebrate Zoology. MVZ had become a major center for the study of natural history under the direction of Joseph Grinnell, whose methods of recording field notes Charles would later use to fill 15 volumes that detailed years of field work in his precise, unedited script. The MVZ maintained an emphasis on the fauna of the region, as well as an association with the museum of paleontology. Accordingly, his first publications were on fossil birds obtained from the tar pits at Rancho La Brea in Los Angeles.

Upon graduation from Berkeley in 1940, with an AB degree in Zoology, Charles worked one year for the federal Public Health Service on plague-suppressive measures. Military service intervened, and he was commissioned as an Ensign in the Navy Reserve. During the later stages of WWII, he was called for active duty, and rose to Lieutenant as a communications officer in the Pacific theater during the last 19 months of the war. His primary station was on Emiru Island (also referred to as Emira and Emirau) in the St. Matthias Group, located 75 miles off the northern tip of the Bismarck Archipelago. During his off-duty time he often collected the local avifauna and sent scientific specimens back to the MVZ. That local collecting effort on Emiru was supplemented while on leave during "R & R" expeditions to the Solomon Islands and the Philippines.

This combination of travel and the collection of scientific specimens was pure pleasure for Charles and would typify family travel experiences over his lifetime. As the years passed, however, the collection of museum specimens was replaced by the collection of egg-white and blood samples for the extraction of DNA. For example, following the 14th International Ornithological Congress in Oxford, Charles organized a month-long European vacation around visits to zoological gardens, aviaries, and the homes of European colleagues in the ongoing effort to obtain critical species for his research.

After the war, and now married to Fran, Charles returned to Berkeley in 1946 to pursue a doctoral degree under the direction of Alden H. Miller, who was himself a protégé of Joseph Grinnell. By the mid 1940s, Miller had followed Grinnell into the Directorship of the MVZ and was particularly interested in species-level taxonomic problems. At that time, Charles met John Davis, another of Miller's incoming doctoral students, whom he joined on a series of collecting trips to Mexico. In later years Charles spoke fondly about those trips and his close friendship with Davis. Perhaps more important, as a result of those experiences Charles became fluent in Spanish, learned the ropes of carrying out field work in Mexico, and was introduced to some peculiar Mexican specimens collected by Helmuth Wagner.

Those specimens turned out to be hybrids between two species of towhee in the genus *Pipilo*. Subsequently, for his doctoral research Charles decided to examine the complex patterns of plumage variation caused by hybridization and the breakdown of species-specific reproductive isolating mechanisms between the "Red-eyed" Towhee (*P. erythrophthalmus*) and the Collared Towhee (*P. ocai*) along the transvolcanic plateau of Mexico. This was a zone of hybridization stretching nearly 500 miles from southeastern Jalisco to the states of Veracruz and Puebla. His thesis, "Species Formation in the Red-eyed Towhees of Mexico," was published as volume 50 of the *University of California Publications in Zoology*, and was the first of 17 of his publications that dealt with avian hybridization.

A major contribution of his doctoral work was the application of a method for summarizing the plumage variation among hybridizing individuals as a single number, a hybrid-index value. The establishment of a species-specific hybrid index was an extraordinarily powerful and ingenious method for analyzing complex, multigenic traits whose morphological patterns shifted geographically due to hybridiza-

tion between incipient species. The method was later used by Charles and his first group of graduate students to study the complex patterns of hybridization between species pairs in the Great Plains of North America. In retrospect, Charles' doctoral research can best be described as an early descriptive stage in the development of his understanding of the role played by hybridization during the process of speciation and as a result of the breakdown of reproductive isolating mechanisms. These were significant contributions, both conceptual and methodological, to our understanding of hybridization as a mechanism of evolution.

After Charles took the position at Cornell University, the hybridization studies were extended to include other species pairs that hybridized throughout the Great Plains of North America. They included Bullock's and Baltimore orioles, Yellow-shafted and Red-shafted flickers, Indigo and Lazuli buntings, and Rose-breasted and Black-headed grosbeaks. Those years were heady, exciting times for him, involving his first graduate students, David A. West, Lester L. Short, Fred C. Sibley (unrelated), and Paul A. Johnsgard in many field trips to collect hybrids along the Platte River, and elsewhere in Colorado, Kansas, Nebraska, and the Dakotas. In addition, the Mexican highlands were revisited to extend his earlier work there.

Although the hybrid-index method had proven to be a powerful tool for studying the complexities of hybridization from the breakdown of reproductive isolation, by 1958 Charles was looking for better ways to quantify the degree of introgression between species pairs. Simultaneously, Paul Johnsgard was in need of financial support to complete his doctoral thesis. In an attempt to resolve both issues, Charles wrote a small proposal to the NSF to examine the possibility of using the new technique of paper electrophoresis to study species-specific variation in the serum proteins of game birds. If successful, it might be applied to the analysis of genetic variation in hybrid populations.

As the research assistant in this small study, Johnsgard followed Charles' instructions to the nth degree . . . almost. It was the "almost" that would prove to be serendipitous. Like most of the students advised by Charles, both then and subsequently, Paul stood in mortal fear of invoking his wrath, should he depart from the protocols carefully prescribed by Charles. Paul, however, had read McCabe and Deutch's earlier paper on the electrophoresis of egg-white proteins. Out of curiosity and a broader interest, but without Charles' consent, Paul began including a few samples of egg whites along with the serum samples during his electrophoretic analyses.

As it turned out, even with the crude technique of paper electrophoresis, the serum-protein electrophoretic patterns seemed much too variable among individuals to be applied to the hybridization studies. (Recall that at that time nothing was known about enzyme variation, either within or between species.) Lamenting this, and greatly discouraged, Charles began to write up the results as a report to the NSF. It was then that Paul mustered the courage to reveal his covert analyses. The egg-white electrophoretic patterns were consistent among individuals of a species, and differed among the few species that had been examined. Charles instantly recognized the implications of those observations. A powerful new tool and a new set of characters were awaiting application by systematists. Almost overnight, he put aside his plans for using serum proteins to study the variation among hybrids, and began to lay plans for an electrophoretic study of egg-white protein variation in birds. Over the subsequent decade and a half, that research would become a massive comparative taxonomic study of the higher avian taxa. Indeed, the relationships among avian orders and families would be at the forefront of his research interests for the remainder of his life. Thus began the next phase of Charles' research, which would overshadow the earlier work throughout the 1960s and into the early 1970s.

The move to electrophoretic analyses of egg-white proteins involved a major shift in Charles' career. Along with Herb Dessauer of Louisiana State University, who studied reptiles and amphibians, and Morris Goodman of Wayne State University, who studied primates, Charles became one of the founders of molecular systematics. For each of these men, this shift required a great deal of retooling, both mentally and in the laboratory. The transition involved a move from activities that primarily used classic field work coupled with comparative morphology to those of daily laboratory

analyses using the methods of comparative biochemistry. As one might expect, the new approach was also encumbered with some of the old thinking.

A peculiar bias that Charles carried concerned the genetic variation of structural proteins versus enzymes and the ways that natural selection would constrain the latter. He, along with one of his colleagues at Cornell, believed that enzymes would be invariant in their amino-acid sequences owing to evolutionary constraints on their activity. Enzymes, in their view, functioned only at specific temperatures and pH values, and natural selection would weed out all but the most effective structure for each enzyme and species. Indeed, during the early 1960s, Charles and his colleague believed that an enzyme's primary structure might prove to be identical both within and among species. Any variation in an enzyme's structure would render it inactive according to their logic, and they knew little about the newly discovered phenomenon of allozymes being studied by Allen C. Wilson at the University of California, Berkeley, and by Clement C. Markert at Johns Hopkins University. Thus, in their view, enzymes would be unlikely to carry phylogenetic information and would be useless for both systematic and population genetics studies. Throughout much of the 1960s, informal debates on this issue occurred between Charles and Allen Wilson.

Wilson's careful studies of allozyme variation, coupled with Markert's research on picine lactate dehydrogenases, eventually convinced Charles that enzymes did in fact vary within species. This change of mind provided the basis for another attempt to study the hybrids of the Great Plains. Although the shift in research was tangential to his main interests, it began in 1969 during the *Alpha Helix* expedition to Papua New Guinea, where the laboratory work took place aboard the ship. The primary thrust of that expedition was to be a general sampling of the fauna of the world's second largest island, but Charles' team also carried out some population genetics studies. Among other research problems, these included hybridizing species pairs within the genus *Paradisea* and non-hybridizing species complexes within the genus *Aplonis*. In fact, among the 22 members of that expedition, nine men focused their activities on different studies of allozyme variation within and among populations. In addition to Charles, who was the prime mover and organizer of the expedition, the molecular systematists were H. C. Dessauer, A. C. Wilson, K. W. Corbin, A. H. Brush, A. Ferguson, J. E. Ahlquist, R. Storez, and V. M. Sarich.

From the outset of that work, Charles was impressed by the analytical results involving two classes of enzymes, the esterases and the dehydrogenases. Both were variable within and among populations, and the frequencies of their variants (i.e. alleles) could be used to characterize individual populations. Within a few weeks of seeing the first electrophoretic results aboard the *Alpha Helix*, Charles began to think about applying the new methods to the hybrids of the Great Plains. He first verbalized these thoughts during one of the field work days in the highlands of Papua New Guinea as he, Corbin, and Ferguson drove along rutted roads in the magnificent forests above Goroka. The approach would be to sample populations of hybridizing species pairs at intervals across the hybrid zone, just as in the earlier studies of plumage variation. This time, however, in addition to the construction of hybrid indices, polymorphic enzymes, esterases perhaps, would be analyzed for their variation by means of electrophoresis. In contrast to the introgression of complex multigenic traits as quantified by hybrid indices, the electrophoretic studies of gene flow would involve single gene traits with simple patterns of inheritance.

The following year those plans began to unfold. The research vessel would be a modern prairie schooner, an Airstream trailer, outfitted with all essential electrophoretic equipment. A full crew was put in the field. After the first week, the collecting focused on orioles and a study of the introgression of genetic variation caused by hybridization between the Bullock's and Baltimore orioles. The results flowed in. Specimens were collected in the mornings and late afternoons; during the midday periods, enzymes were extracted and analyzed by means of starch-gel electrophoresis. The data base mounted and soon became impressive, encouraging the collecting party westward in 50-mile leaps across the zone of hybridization, and then back eastward, filling in the gaps between the initial collecting localities.

That summer's collecting continued in 1971 and 1974. The results of the population genetics

analyses confirmed the earlier morphological studies. Gene flow across the Great Plains was extensive, at least among populations of orioles. Alleles at esterase loci were being exchanged between the eastern and western populations, just as the plumage characters flowed eastward and westward through the filter of the zone of hybrids along the Platte River in Nebraska and Colorado. Presumably, gene flow was comparable in the other riparian habitats stretching across the Great Plains, although Charles' studies of the patterns of hybridization in Mexican towhees showed that such assumptions might be unwarranted. Nevertheless, these and studies by others revealed that the "species" of these hybridizing species pairs might in fact be subspecies. This recognition was reflected in later versions of the *AOU Check-list of North American Birds.* The research on hybridization ceased after 1974, and thus ended Charles' research on species-level taxonomic problems.

By 1974, Charles was already a decade and a half into the taxonomic comparison of egg-white proteins. The early electrophoretic methods for the separations of proteins on paper strips soon became obsolete as more sophisticated technology was developed. Paper electrophoresis gave way to starch-gel electrophoresis, whose relatively crude resolution potential was supplanted by polyacrylamide gel electrophoresis and eventually by isoelectric focusing in either polyacrylamide gels or in agarose plates. In an ongoing attempt to refine and improve the quality of his comparative data, Charles adopted each new development almost as soon as it became commercially available.

Early on he was convinced that the comparative study of protein variation could aid significantly in determining avian phylogenetic relationships at the higher levels of classification. He was equally certain that the methods would not be much help at the levels of species and genera. Although protein differences were basically phenotypic characters, they differed in one significant way from the traditional morphological characters used by most systematists at that time. Namely, protein structure, determined by amino-acid sequences, was only one step removed from the genetic code itself. Consequently, differences among proteins were a more direct reflection of the underlying genetic similarities and differences among species than was gross morphology. It was this relationship between genes and the traits they encoded, in this case the primary structure of proteins, that convinced Charles he was on the right track.

The first results of the early electrophoretic studies suggested that the relationships among the higher taxa could be determined with relative ease. The protocols were simple: obtain egg white from the species of interest, separate the proteins of each sample on either starch or polyacrylamide gels under appropriate controls and standard electrophoretic conditions of wattage and time, stain the gels with amido blue black, photograph the gels, and then compare the resulting patterns. Voila! Evolutionary relationships were revealed like never before. It was a heady time, and the world was watching and waiting for the results. Some were envious that Charles was making such headway in solving age-old taxonomic problems, others were bitter that their own expertise was being eclipsed, but most ornithologists were enthusiastic about the progress being made.

By as early as 1959, the Cornell laboratory was deeply involved in a comparative study of the egg-white proteins by means of acrylamide gel electrophoresis in small glass tubes. Soon thereafter, and with his usual skill, energy, and enthusiasm, Charles was extolling the virtues of those data in resolving long-standing systematic problems. At annual scientific meetings and during invited lectures in North America and Europe he began to spread the message about the wonders of the new comparative methods. In 1960, he eagerly presented data that demonstrated the affinities of the Old World sylviids and muscicapids in contrast to their more distant New World cousins, the parulids. By the time of the 13th International Ornithological Congress (1962), which was held in Ithaca with Charles as Secretary General, there were electrophoretic data bearing upon the relationships of many more avian families.

The methods of electrophoretic analysis may have been relatively uncomplicated, but the effort to examine the evolutionary relationships of all the higher avian taxa by means of electrophoresis was daunting. There were the nests of thousands of species to find. Each egg-white specimen had to be compared electrophoretically over and over again. Thousands of analyses were carried out over almost two decades.

Nothing but unequivocal data would satisfy Charles' objectives. How else could one compare all of the higher avian taxa by means of this new technology? The museums of the world housed the scientific specimens needed for comparative morphological studies, but there were no depositories of egg-white specimens. Every species used in Charles' research program had to be collected by him and his collaborators.

Charles set out to do that, encouraging volunteers from throughout the world to collect samples and ship them to Cornell University. The effort was massive and profoundly successful. For more than a decade the samples came in from every continent. Willing students acquired collecting permits, risked their necks climbing trees and cliff faces, combed forests, prairies, and tundra, all in search of samples from both common and rare species. Hosts of both professional ornithologists and amateur birders collaborated in the effort. Along the way more than a dozen technicians carried out the lab work that was completed at Cornell and at Yale. The effort was monumental and culminated in two monographs published by the Peabody Museum of Natural History at Yale. The first, authored by Charles alone, *A Comparative Study of the Egg White Proteins of Passerine Birds,* was published in 1970, and the second, coauthored with J. E. Ahlquist, *A Comparative Study of the Egg White Proteins of Non-passerine Birds,* was published in 1972. Charles was proud of these publications, as well he should have been. Many taxonomic problems were resolved, although others remained.

In addition to the studies of egg-white proteins, there were side excursions to use other protein systems, either by way of confirmation or for specific taxonomic problems. One of these, coauthored with A. H. Brush, involved an extensive study based on the electrophoretic variation of eye-lens proteins. Another, coauthored with H. T. Hendrickson, involved the plasma proteins. Two particularly intractable taxonomic problems, one involving the relationships of the flamingoes (Sibley, Corbin, and J. H. Haavie), and the other the relationships of the seedsnipes (Sibley, Corbin, and Ahlquist), were tackled by using ion-exchange column chromatographic techniques to examine variation in the tryptic peptides of their hemoglobins. Other studies were never published. The most important of these was a massive data base developed during the early years at Yale. It dealt with the electrophoretic variation of avian hemoglobins, and samples were obtained from more than half of the then recognized species of the world's birds. Another study involved an attempt to use serology to examine the blood-serum proteins of muscicapids and sylviids. Ultimately, however, it was the study of the egg-white proteins that paid the highest dividends.

The egg-white studies of the birds of the world, following those of avian hybridization on the Great Plains, would have been a life's work for most individuals in academia, but not for Charles. As the successes of the electrophoretic analyses of the egg-white proteins began to accumulate, a new technique was being tested in his laboratories at Cornell and later at Yale. The method's early development by others was an attempt to examine differences in DNA molecules by means of annealing, or hybridizing, short fragments of DNA to one another. The technique soon became known as DNA-DNA hybridization. Although Charles' laboratory at Cornell began to explore the potential of this method as early as 1963, another decade would pass before Charles had perfected the "DNA machine" in his laboratories at Yale.

The DNA-DNA hybridization studies involved the development of another tissue collection. Initially, while at Cornell, an attempt was made to use methods of tissue culture to grow avian fibroblasts obtained from embryos. This method was soon discarded because of technical problems, coupled with the fact that a more direct method was available. Because birds have nucleated red blood cells, blood samples were the obvious and expedient source of avian DNA. By the mid-1970s, studies of the proteins of egg whites, blood, and eye lenses were all but complete; it was time for the DNA studies to begin in earnest.

The years at Yale were some of the best for Charles and some of his worst. The best saw the publication of his egg-white monographs by the Peabody Museum of Natural History and the development of the DNA-DNA hybridization data base. By 1986, the latter was being used to piece together a comprehensive phylogeny of the orders and families of the birds of the world. In printed form the dendrogram spanned more than 20 feet along the walls of

poster sessions held in conjunction with annual scientific meetings during the 1980s. It thus became known as the "tapestry" and was a phenomenon in itself, as groups of people simultaneously examined its details.

The worst moments at Yale involved allegations against Charles for two kinds of scientific impropriety. The first was a federal indictment alleging that he had illegally imported the egg whites of six European species, including one that was wholly fictitious and contrived by unknown individuals, either within or outside of the U.S. Fish and Wildlife Service. After a good deal of media attention, and the paying of a substantial fine, this episode eventually led to Charles' resignation of the directorship of the Peabody Museum of Natural History. It was a sad moment, indeed, for a man who had operated within the federal guidelines and with all required scientific collecting permits in hand more than 99 percent of the time. It was also a black mark against the scientific community that did so little to protest this injustice against one of their own who had made such significant contributions to the field of systematics.

From a scientific point of view, the second allegation was much more serious. It involved the informal charge that the analyses of DNA-DNA hybridization data had been manipulated to yield results that conformed with preconceived notions of phylogenetic relationships. One could argue that the methods of data analysis were not as rigorous as they might have been, and there were certainly differences of opinion among the members of Charles' own research group on how best to quantify and summarize the data, but that does not constitute fraud. In fact, the issue probably would never have arisen had not Charles and his group ventured into the treacherous waters involving human evolution. The debates in that arena are legendary, beginning with Raymond Dart and leading up to today's antagonists. In Charles' case, the issue revolved around rates of genetic change along different phylogenetic lineages, one of which led to our species, and others of which led to primate species whose relationship to us was hotly debated. It was this debate that focused the attention of the scientific community on Charles' preferred methods of analysis of the DNA hybridization data. At its heart, the issue was whether evolution, with respect to the entire genome of an organism, does indeed occur at a constant average rate, as Charles maintained. Although solid evidence exists to suggest that rates of change differ among different lineages, the jury is still out on this issue.

As in all other matters of his life, Charles believed in himself. He believed, unequivocally, that his analyses of the relationships of the birds of the world were correct. Two massive scientific contributions were published by Yale University Press in 1990. One, in collaboration with his close friend and colleague, Burt Monroe, Jr., was *Distribution and Taxonomy of the Birds of the World,* a comprehensive treatment of all avian species recognized as of 1990. The other, with his long-time associate, Jon E. Ahlquist, was *Phylogeny and Classification of the Birds of the World: A Study in Molecular Evolution.* This was the tapestry, along with all of the supporting data.

Charles knew the history of systematics well. He knew better than most of us that classifications were always under review and modification, and so he did not delude himself into believing that his classification would be the final word on avian taxonomy. One of his dreams, however, during the early phase of the DNA research, was to be able to read off nucleotide sequences from a DNA molecule. That was the kind of precision he sought, knowing full well that the technology of the 1970s and 1980s was not up to the task. Today, however, automatic DNA sequencing methods produce long sequences of nucleotides, and genome projects are well advanced for humans, cows, pigs, and *Drosophila.* Indeed, in 1998 the sequencing of the entire genome of a multicellular organism, the round worm *C. elegans,* was completed. We can be certain, therefore, that future generations of avian systematists will build upon the many contributions made by Charles and his group, perhaps finally reaching a consensus with regard to the phylogenetic relationships of avian orders, families, and even genera.

Charles Sibley passed away in Santa Rosa, California, on Easter Sunday, 12 April 1998, due to myelogenous leukemia.